

THE OPERCULUM OF THE GENUS *BURSA* (*RANELLA*).

By the Rev. A. H. COOKE, Sc.D., F.Z.S.

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W. H. DALL, in his well-known and admirable paper,¹ "An Historical and Systematic Review of the Frog-Shells and Tritons," draws up a classification, which results in the following grouping:—

Genus *BURSA*.A. Sub-genus *Bursa*.

Operculum with lateral nucleus:

- (a) Sect. *Bursa* (*spinosa*, Lam.).
- (b) Sect. *Marsupina* (*spadicea*, Mtf., or *crassa*, Dillw.).
- (c) Sect. *Chasmotheca* (*foliata*, Brod.).

Operculum with apical nucleus:

- (d) Sect. *Ranella* (*bufonia*, Gmel.).
- (e) Sect. *Lampadopsis* (*rhodostoma*, Beck.).
- (f) Sect. *Colubrellina* (*conditus*, Gmel.).

B. Sub-genus *Aspa*.Sect. *Aspa* (*marginata*, Gmel.).C. Sub-genus *Bufonaria*.

- (a) Sect. *Crossata* (*ventricosa*, Brod.).
- (b) Sect. *Bufonaria* (*scrobilator* [*sic*], L.).
- (c) Sect. *Craspedotriton* (*convolutus*, Brod.).

It will be noticed that the characteristics of the operculum, given in the above classification, affect only one of the three sub-genera (*Bursa*), while of the operculum of the two remaining sub-genera (*Aspa*, *Bufonaria*) nothing is stated.

Dall further remarks: "According to Adams the *Ranella* have the operculum ovate, with an apical or subapical nucleus, while Gray speaks of it as half-ovate with a central, lateral, or internal nucleus; probably it varies in the different groups as in the Tritons; in *Ranella foliata* it is figured as concentric, with the nucleus mid-lateral. One cannot safely generalize on the character until the operculum of more species is known."

In view of this last remark I venture to put on record the facts, so far as they are known to me, of a considerable number of species of the genus *Bursa*. If students to whom are known the opercula of other species not in the list will gradually add to the number, a more or less complete body of evidence will in the end be accumulated. No final classification of a group can be regarded as settled until full information of this kind is in our possession.

It must be premised that Dall published no list of species contained in each of his several groups or sections, but only a type species in each case. I have therefore worked the list as interpreted by the

¹ Smiths. Coll., xlvii, 1904, pp. 114-44.

Natural History Museum in their show-cases. The only difference between their grouping and Dall's is the nominal substitution of *Tutufa*, Jous., for the sub-genus he calls *Bufonaria*.

Nothing is commoner than for opercula to be misplaced, turned upside down, outside in, and even located in shells they do not belong to. Great caution is needed in order to avoid mistakes.

Species whose operculum is known.	Source of information. ¹	Species whose operculum is not known.
Sub-genus <i>Bursa</i> .		
Sect. <i>Bursa</i> .		
<i>albifasciata</i> , Sowb.	M.B.	<i>cavitensis</i> , Beck.
<i>crumena</i> , Lam.	M.M., J.R.T.	<i>fijiensis</i> , Wats.
<i>elegans</i> , Beck.	Ph.D., J.R.T., A.H.C.	<i>neglecta</i> , Sowb.
<i>margaritula</i> , Desh.	J.R.T., A.H.C.	<i>nobilis</i> , Rve.
<i>nana</i> , Sowb.	M.B.	
<i>rana</i> , L.		
(= <i>albifasciata</i> , Rve.)	McA., A.H.C.	
<i>spinosa</i> , Lam.	M.M., J.C.M., A.H.C.	
<i>thersites</i> , Redf.	J.C.M.	
Sect. <i>Marsupina</i> .		
		<i>crassa</i> , Dillw.
Sect. <i>Chasmotheca</i> .		
		<i>foliata</i> , Brod.
Sect. <i>Ranella</i> .		
<i>bufonia</i> , Lam.	M.B., A.H.C.	<i>grayana</i> , Dkr.
<i>siphonata</i> , Rve.	J.C.M., A.H.C.	<i>rugosa</i> , Sowb.
<i>tuberosissima</i> , Rve.	A.H.C.	<i>venustula</i> , Rve.
Sect. <i>Lampadopsis</i> .		
<i>asperrima</i> , Dkr.	M.B.	<i>papilla</i> , Wood.
<i>cruentata</i> , Sowb.	Ph.D., J.R.T.	
<i>rhodostoma</i> , Desh.	Ph.D., A.H.C.	
<i>thomæ</i> , Orb.	M.B.	
Sect. <i>Colubrellina</i> .		
<i>cælata</i> , Brod.	M.B., A.H.C.	<i>caudisata</i> , Lam.
<i>granularis</i> , Bolt.	M.B., M.M.	(= <i>condita</i> , Dillw.).
var. <i>affinis</i> , Brod.	M.M., J.R.T.	
var. <i>livida</i> , Rve.	Ph.D., M.M.	
var. <i>ponderosa</i> .	Ph.D.	
<i>pustulosa</i> , Rve.	M.B.	
<i>semigranosa</i> , Lam.	J.R.T.	
Sub-genus <i>Aspa</i> .		
Sect. <i>Aspa</i> .		
<i>marginata</i> , Gmel.	M.B., McA., A.H.C.	

¹ In this list, M.B., M.M. mean the British and Manchester Museums, McA. the McAndrew Collection at Cambridge, J.C.M., J.R.T., Ph.D., A.H.C. mean respectively Dr. J. C. Melvill's, Mr. Tomlin's, M. Dautzenberg's, and my own collections.

Species whose operculum is known.	Source of information.	Species whose operculum is not known.
Sub-genus <i>Bufonaria</i> (= <i>Tutufa</i> , Jous.).		
Sect. <i>Crossata</i> .		
<i>californica</i> , Hinds.	M.B., McA., A.H.C.	
<i>ventricosa</i> , Brod.	J.R.T., A.H.C.	
Sect. <i>Bufonaria</i> .		
<i>rubeta</i> , Bolt.	M.B.	<i>coriacea</i> , Rve.
<i>serobiculator</i> , L.	J.C.M., J.R.T.	<i>cumingiana</i> , Dkr. <i>papillosa</i> , A. Ad. <i>ranelloides</i> , Rve.

With regard to the section *Craspedotriton*, Kesteven has shown¹ that the operculum and radula of *convolutus*, Brod., are those of *Trophon*, not *Bursa*; it is probable, therefore, that *scalariformis*, Brod., and *scalarina*, A. Ad. (= *speciosa*, Ang.), will also prove to be *Trophons*: the section therefore drops out.

The details of the known species are as follows:—

A. Sub-genus *BURSA*.

(a) Section *Bursa*.

General characteristics: operculum rather thin, more or less transparent, almost triangular, with longer side rounded, nucleus sub-lateral, to the left (*i.e.* adjacent to the columella), nearly central, clear of the margin, lines of growth prominent.

1. *albifasciata*, Sowb. A somewhat broken operculum is attached to the tablet in M.B., nucleus to right, sub-lateral, half-way between centre and lower end. In other words, if the operculum belongs to the shell, which I doubt (the shells are Cuming's), the species must be removed, probably to section *Ranella* or *Colubrellina*, from which, conchologically, it is quite distinct.

2. *crumena*, Lam. Nucleus well marked, lines of growth flattened.

3. *elegans*, Beck. As in *spinosa*, not transparent, colour deep brown.

4. *margaritula*, Desh. Rather less pointed at top and bottom than the other species, dark brown, lines of growth not very prominent.

5. *nana*, Sowb. Two opercula are attached to the tablet in M.B. (Cuming's specimens), one rather long, narrow, nucleus sub-terminal, the other more ovate, light-coloured, nucleus sub-marginal, to right, below the centre. It is clear that both of these cannot be the true opercula, and I am inclined to regard them both with suspicion.

6. *rana*, L. Thin, transparent, lines of growth very sharply marked, and occasionally rising into broad raised ridges.

7. *spinosa*, Lam. Not angled, but rounded, against the columella, thicker than in *rana*, lines of growth not elevated.

8. *thersites*, Redf. Rather thin, nucleus very near the margin, a little below the centre.

¹ Proc. Linn. Soc. N.S. Wales, vol. xxvii, 1902, p. 479. Dall, though writing his paper on the Frog Shells in 1904, does not seem to have seen Kesteven's paper, as he expressly says (p. 13), with reference to *scalariformis* and *convolutus*, "their operculum is not known to me."

Sections *Marsupina* and *Chasmotheca*.

It seems doubtful whether these sections embody any valid distinction from *Bursa*, s.str. The operculum of *crassa*, Dillw., does not appear to be known; Dall states that that of *foliata* is as in *rana*.

(b) Section *Ranella*.

General characteristics: nucleus to right, thicker than in *Bursa*, not well marked, lateral, sub-terminal.

1. *bufonia*, Lam. Rounded above, narrower below, nucleus very indistinct, close to the right of terminal margin.

2. *siphonata*, Rve. Rounded above and below, nucleus better marked and rather higher up than in *bufonia*.

3. *tuberosissima*, Rve. Almost exactly as in *siphonata*.

(c) Section *Lampadopsis*.

General characteristics: more or less as in *Ranella*.

1. *asperrima*, Dunk. Thin, ovate, transparent horn-colour, nucleus terminal, well marked, slightly to the left, lines of growth well marked. This operculum differs markedly in character from the others in the section.

2. *eruentata*, Sowb. Thin, rounded above, somewhat angled below, nucleus sub-terminal, to right, fairly well marked.

3. *rhodostoma*, Desh. "Nucleus lateral, submarginal, to the right and sub-terminal, like that of *siphonata*" (Ph.D.).

4. *thomæ*, Orb. Thin, ovate, nucleus sub-marginal, to the left, sub-terminal, indistinctly marked.

(d) Section *Colubrellina*.

General characteristics: operculum ovate, sometimes semi-unguiculate, thickish, narrower below than above, nucleus rather obscure, sub-terminal, or sub-lateral to the right.

1. *granularis*, Bolt., with vars. *affinis*, Brod., *livida*, Rve., *ponderosa*, Rve. The nucleus varies slightly in position; in two typical *granularis* (= *granifera*, Lam.) from M.M. the nucleus is sub-terminal, in a *livida* from M.M. and an *affinis* from J.R.T. it is obscurely sub-marginal, to the right, and sub-terminal. Ph.D. remarks to me: "operc. à nucléus latéral, marginal, situé, soit au dessous du milieu, soit même presque à l'extrémité."

2. *cælata*, Brod. Shape almost semi-unguiculate, nucleus well marked, sub-terminal, but well away from the margin, lines of growth well marked, rising into ridges in old specimens.

3. *pustulosa*,¹ Rve. Shape semi-unguiculate, nucleus almost terminal, closely resembling that of *cælata*.

4. *semigranosa*, Lam. Many consider this species another variety of *granularis*. Operculum thin, nucleus obscure, sub-marginal, to right, sub-terminal, as in *granularis*.

¹ This species, from West Africa, St. Helena, and Ascension, must surely be regarded as distinct from *cælata*, Brod., a Panama shell which does not occur in the West Indies.

B. Sub-genus *Aspa*.Section *Aspa*.

marginata, Gmel. (the only species). Operculum thin, semi-transparent, lines of growth clearly marked. Shape as in *Bursa*, but not so triangular, nucleus similarly situated, slightly more removed from the left margin.

C. Sub-genus *Bufo**naria*.(a) Section *Crossata*.

General characteristics: operculum ovate, rounded at both ends, thick, dark horn-colour, lines of growth obscure, a nucleus indicated but not existing, lateral, sub-terminal, to right.

1. *californica*, Hinds. Operculum as in the section. In a remarkably fine and clear specimen from McA. there is almost a visible nucleus on the margin low down on the right.

2. *ventricosa*, Brod. Operculum a little wider than in *californica*, but in other respects generally corresponding.

(b) Section *Bufo**naria* (= *Tutufa*, Jous.).

1. *rubeta*, Bolt. (= *lumpas*, auctt.). Operculum sub-ovate, not very thick, rounded at top, angled below, nucleus distinct, sub-lateral, to right, well away from margin, below the centre, lines of growth well marked, but not raised in ridges.

2. *scrobiculator*, L. Operculum sub-ovate, rather thin, semi-transparent, rounded above and below, nucleus distinct, sub-lateral, to right, well away from margin, below centre, lines of growth well marked, but not raised in ridges.

On a general survey of the evidence afforded by the operculum, the following points seem to stand out:—

1. There is a large group of *Bursa* (*Bursa*, s.str. + *Chasmotheca* + ? *Marsupina*) with a more or less triangular operculum, nucleus well marked, in the centre of the *left* sub-margin.

2. Closely allied to this group stands the sub-genus *Aspa*, conchologically different, but with an operculum of similar general construction.

3. Another large group (*Ranella* + *Lampadopsis* + *Colubrellina*) possesses an ovate operculum, with nucleus to the *right* or near the extremity, generally less well marked, sub-marginal or sub-terminal. Closely allied to this group, and possibly not separable from it, are the species contained in section *Bufo**naria*.

4. Further removed comes a group (*Crossata*) geographically separate from the *Bufo**naria* section, and with an operculum not essentially dissimilar to that of certain species of *Triton* (*Iotorium*).

As Dall has remarked, "the *Ranellas* shade very gradually into the forms formerly known as *Triton*, judged by most of their characters," and it is interesting to observe how, on the one hand, *Gyrineum* and *Eugyrina* carry the "*Ranella*" shape of shell, minus the anal sulcus, into the "*Tritons*", while the shell shape of certain

low-spined forms of *Lotorium* is carried into the *Crossata* group of "*Ranella*".

The evidence, then, of the operculum, plus certain other considerations which have appeared in this paper, would lead one to throw out the suggestion that perhaps Dall's classification might with advantage be modified in the following way:—

A. Sub-genus *BURSA*, containing in a single section *Bursa*, s.str., *Chasmotheca*, and probably *Marsupina*.

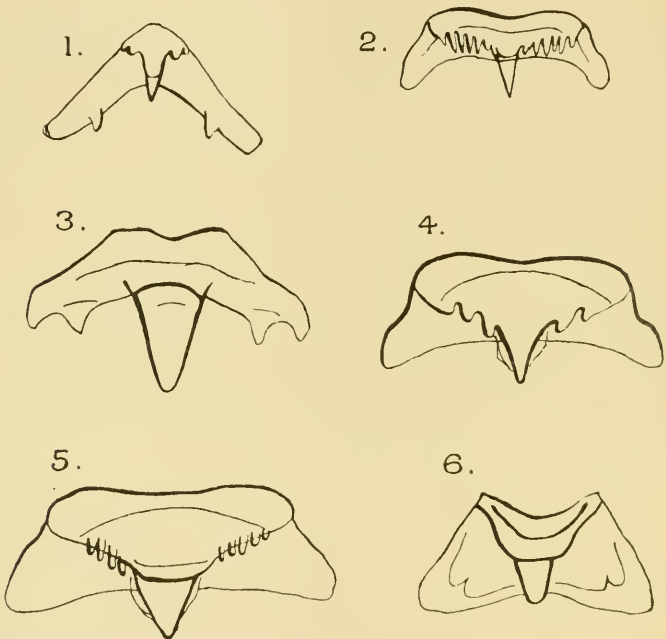


FIG. 1.—Median teeth of:—1. *Bursa granularis*, Bolt., Umkomaas, Natal. 2. *Triton (Lotorium) australis*, Lam., Port Jackson. 3. *Crossata ventricosa*, Brod., Orange Harbour, Tierra del Fuego. 4. (*Triton*) *leucostoma*, Lam., Port Shepstone. 5. *Eugyrina gigantea*, Lam., Algiers. 6. *Crossata californica*, Hinds, San Pedro, Cal. All from Professor Gwatkin's collection.

B. Sub-genus *ASPA*.

C. A sub-genus (*RANELLA* would be a convenient title) including all the sections whose operculum is sub-marginal, generally but not always to the right, or sub-terminal, viz. *Ranella*, *Lampadopsis*, *Colubrellina*, and *Bufonaria*.

D. A sub-genus (call it *CROSSATA* if you like) including the two species *californica* and *ventricosa*, the form of whose shell and shape of whose operculum approximate towards the "*Tritons*".

The evidence of the radula, as kindly given to me by Professor H. M. Gwatkin, may be stated thus:—

An examination of twenty-six species and varieties shows three types of radula.

1. A *Bursa* type, which includes all the typical *Bursæ*, viz. *bufonia*, *celata*, *cruentata*, *crumena*, *granularis* and varieties, *pustulosa*, *rana*, *rhodostoma*, *semigranosa*, *siphonata*, *spinosa*, *thomæ*.

Under this type also, but somewhat distinct from it, come (*a*) *marginata*, with radula of so delicate proportions that it stands somewhat apart from the others, and (*b*) *rubeta*, of the typical form, but much stronger and stouter.

2. A Triton (*Lotorium*) type (i.e. a median tooth with strong central denticle and several small side denticles) including *perca*, *pusilla*, *tuberculata*, *vevillum*, and *argus*, but not *gigantea* or *leucostoma*. (N.B. These radulæ of the "Triton" type are by no means typical "Tritons".)

3. A type unlike both *Bursa* and "Triton" proper, and including *californica*, *ventricosa*, *gigantea*, and *leucostoma*. The median exhibits one great central denticle, and is almost bare of side denticles in *californica* and *gigantea*: *ventricosa* combines the big central denticle with the lateral prolongations of a *Bursa* (Fig. 1).

I have to express my thanks to Mr. R. Standen, of the Manchester Museum, to the authorities of the Museum of Zoology at Cambridge, to Dr. J. C. Melvill, and Mr. J. R. Le B. Tomlin for the kind loan of specimens, now exhibited, and also to M. Ph. Dautzenberg for valuable information.